Great ideas in ecology for the 1990s

In a commentary entitled "Science literacy" (Pool 1991), there is a table of "Science's top 20 greatest hits" as chosen by biologist Robert Hazen and physicist James Trefil. They suggested that these "great ideas" might be the basis for a course in general science, and comments from readers were invited.

In addition to the two laws of thermodynamics, Hazen and Trefil's list includes three other concepts that could be construed as ecological. These concepts are "everything on earth operates in cycles," "all forms of life evolved by natural selection," and "all life is connected."

For many years, I have contended that ecology is no longer a subdivision of biology but has emerged from its roots in biology to become a separate discipline that integrates organisms, the physical environment, and humans—in line with *oikos*, root of the word *ecology* (Odum 1977). From this view, the ecosystem level becomes the major focus. Populations are considered as ecosystem components and landscapes as associations of interacting ecosystems. This viewpoint is now generally accepted, as was indicated by a recent British Ecological Society survey in which members were asked to list what they considered the most important ecological concepts. The ecosystem was the concept most frequently listed (Cherrett 1989).

At the time that the science literacy article appeared, I was drawing up a list of basic concepts in ecology that might be included in courses designed to improve environmental literacy among undergraduates here at the University of Georgia. Here are 20 of my "great ideas" in ecology, as distinguished from "great ideas" in biology (e.g., DNA, genetic code, and general theory of natural selection). The last five items in my list relate to human ecology and the ecology-economics interface, which must be major foci in environmental literacy education in view of the increasingly serious global impacts resulting from human activities. The references I have selected for each concept may not be the best ones, and certainly they are not the only ones.

by Eugene P. Odum

Concept 1. An ecosystem is a thermodynamically open, far from equilibrium, system. Input and output environments are an essential part of this concept. For example, in considering a forest tract, what is coming in and going out is as important as what is inside the tract. The same holds for a city. It is not a self-contained unit ecologically or economically; its future depends as much on the external life-support environment as on activities within city limits (Odum 1983, Patton 1972, Prigogine et al. 1972).

Concept 2. The source-sink concept: one area or population (the source) exports to another area or population (the sink). This statement is a corollary to concept 1. It is applicable at ecosystem as well as population levels. At the ecosystem level, an area of high productivity (salt marsh, for example) may feed an area of low productivity (adjacent coastal waters). At the population level, a species in one area may have a higher reproduction rate than needed to sustain the population, and surplus individuals may provide recruitment for an adjacent area of low re-production. Food chains may also involve sources and sinks (see concept 12; Lewin 1989, Pulliam 1988).

Concept 3. In hierarchical organization of ecosystems, species interactions that tend to be unstable, nonequilibrium, or even chaotic are constrained by the slower interactions that characterize large systems. Short-term interactions, such as interspecific competition—the evolutionary arms race between a parasite and its host, herbivore-plant interactions, and predator-prey activites—tend to be oscillatory or cyclic. Large, complex systems—such as oceans, the atmosphere, soils, and large forests—tend to go from randomness to order and will tend to have more steady-state characteristics, for example, the atmosphere's gaseous balances.

Accordingly, large ecosystems tend to be more homeostatic than their components. This principle may be the most important of all, because it warns that what is true at one level may or may not be true at another level of organization. Also, if we are serious about sustainability, we must raise our focus in management and planning to large landscapes and beyond (Allen and Starr 1982, Kauffman 1990, O'Neill et al. 1986, Prigogine and Stengers 1984, Ulanowicz 1986).

Concept 4. The first signs of environmental stress usually occur at the population level, affecting especially sensitive species. If there is sufficient redundancy, other species may fill the functional niche occupied by the sensitive species. Even so, this early warning should not be ignored, because the backup components may not be as efficient. When the stress produces detectable ecosystem-level effects, the health and survival of the whole system is in jeopardy. This idea is a corollary of item 3: parts are less stable than wholes (Odum 1985, 1990, Schindler 1990).

Concept 5. Feedback in an ecosystem is internal and has no fixed goal. There are no thermostats, chemostats, or other set-point controls in the biosphere. Cybernetics at the ecosystem level thus differs from that at the organism level (body temperature control, for example) or that of human-made mechanical systems (temperature control of a building, for example) where the control is external with a set point. Ecosystem control, where manifested, is the result of a network of internal feedback processes as yet little understood—another corollary of concept 3 (Patten and Odum 1981).

Concept 6. Natural selection may occur at more than one level. This idea is another corollary to concept 3. Accordingly, coevolution, group selection, and traditional Darwinism are all part of the hierarchical theory of evolution. Not only is the evolution of a species affected by the evolution of interacting species, but a species that benefits its community has survival value greater than a species that does not (Axelrod 1984, 1980, Axelrod and Hamilton 1981, Gould 1982, Wilson 1976, 1980).

Concept 7. There are two kinds of natural selection, or two aspects of the struggle for existence: organism versus organism, which leads to competition, and organism versus environment, which leads to mutualism. To survive, an organism does not compete with its environment as it might with another organism, but it must adapt to or modify its environment and its community in a cooperative manner. This concept was first suggested by Peter Kropotkin soon after Darwin. (Gould 1988, Kropotkin 1902).

Concept 8. Competition may lead to diversity rather than to extinction. Although competition plays a major role in shaping the species composition of biotic communities, competition exclusion (in which one species eliminates another, as in a flour beetle microcosm) is probably the exception rather than the rule in the open systems of nature. There, species are often able to shift their functional niches to avoid the deleterious effects of competition (den Boer 1986).

Concept 9. Evolution of mutualism increases when resources become scarce. Cooperation between species for mutual benefit has special survival value when resources become tied up in the biomass, as in mature forests, or when the soil or water is nutrient poor, as in some coral reefs or rainforests (Boucher et al. 1982, Odum and Biever 1984). The recent shift from confrontation to cooperation among the world's superpower nations may be a parallel in societal evolution (Kolodziej 1991).

Concept 10. Indirect effects may be as important as direct interactions in a food web and may contribute to network mutualism. When food chains function in food web networks, organisms at each end of a trophic series (for example, plankton and bass in a pond) do not interact directly but indirectly benefit each other. Bass benefit by eating planktiverous fish supported by the plankton, whereas plankton benefit when bass reduce the population of its predators. Accordingly, there are both negative (predator-prey) and positive (mutualistic) interactions in a food web network (Patton 1991, Wilson 1986).

Concept 11. Since the beginning of life ôn Earth, organisms have not only adapted to physical conditions but have modified the environment in ways that have proven to be beneficial to life in general (e.g., increase O_2 and reduce CO_2). This modified Gaia hypothesis is now accepted by many scientists. Especially important is the theory that microorganisms play major roles in vital nutrient cycles (especially the nitrogen cycle) and in atmospheric and oceanic homeostasis (Cloud 1988, Lovelock 1979, 1988, Kerr 1988, Margulis and Olendzenski 1991).

Concept 12. Heterotrophs may control energy flow in food webs. For example, in warm waters, bacteria may function as a sink in that they short-circuit energy flow so that less energy reaches the ocean bottom to support demersal fisheries. In cooler waters, bacteria are less active, allowing more of the fruits of primary production to reach the bottom (Pomeroy 1974, Pomeroy and Deibel 1986, Pomeroy and Wiebe 1988). Small hetertrophs may play similar controlling roles in terrestrial ecosystems such as grasslands (Dyer et al. 1982, 1986, Seastadt and Crossley 1984). This concept is a corollary of concept 11.

Concept 13. An expanded approach to biodiversity should include genetic and landscape diversity, not just species diversity. The focus on preserving biodiversity must be at the landscape level, because the variety of species in any region depends on the size, variety, and dynamics of patches (ecosystems) and corridors (Odum 1982, Turner 1988, Wilson 1988).

Concept 14. Ecosystem development or autogenic ecological succession is a two-phase process. Early or pioneer stages tend to be stochastic as opportunistic species colonize, but later stages tend to be more self-organized (perhaps another corollary of concept 3; Odum 1989a).

Concept 15. Carrying capacity is a two-dimensional concept involving number of users and intensity of per capita use. These characteristics track in a reciprocal manner—as the intensity of per capita impact goes up, the number of individuals that can be supported by a given resource base goes down (Catton 1987). Recognition of this principle is important in estimating human carrying capacity at different quality-of-life levels and in determining how much buffer natural environment to set aside in land-use planning.

Concept 16. Input management is the only way to deal with nonpoint pollution. Reducing waste in developed countries by source reduction of the pollutants will not only reduce global-scale pollution but will spare resources needed to improve quality of life in undeveloped countries (Odum 1987, 1989b).

Concept 17. An expenditure of energy is always required to produce or maintain an energy flow or a material cycle. According to this net-energy concept, communities and systems, whether natural or human-made, as they become larger and more complex, require more of the available energy for maintenance (the so-called complexity theory). For example, when a city doubles in size, more than double the energy (and taxes) is required to maintain order (Odum and Odum 1981, Pippenger 1978).

Concept 18. There is an urgent need to bridge the gaps between human-made and natural life-support goods and services and between non-sustainable short-term and sustainable long-term management. Agroecosystems, tropical forests, and cities are of special concern. H. T. Odum's "emergy" concept and Daly and Cobb's index of sustainable economic welfare are examples of recent attempts to bridge these gaps (Daly and Cobb 1989, Folke and Kaberger 1991, Holden 1990, Odum 1988).

Concept 19. Transition costs are always associated with major changes in nature and in human affairs. Society has to decide who pays, for example, the cost of new equipment, procedures, and education in changing from high-input to low-input farming or in converting from air polluting to clean power plants (Renner 1991, Spencer et al. 1986).

Concept 20. A parasite-host model for man and the biosphere is a basis for turning from exploiting the earth to taking care of it (going from dominionship to stewardship, to use a biblical metaphor). Despite, or perhaps because of, technological achievements, humans remain parasitic on the biosphere for life support. Survival of a parasite depends on reducing virulence and establishing reward feedback that benefits the host (Alexander 1981, Anderson and May 1981, 1982, Levin and Pimentel 1981, Pimentel 1968, Pimentel and Stone 1968, Washburn et al. 1991). Similar relationships hold for herbivory and predation (Dyer et al. 1986, Lewin 1989, Owen and Wiegert 1976). In terms of human affairs, this concept involves reducing wastes and destruction of resources to reduce human virulence, promote the sustainability of renewable resources, and invest more in Earth care.

Concept comparisons

In my list, I have covered the ecological items in Hazen and Trefil's "great ideas in science." Thermodynamics is represented in concept 1, natural selection in concepts 6 and 7 (and indirectly in most others), and cyclic behavior and connectiveness in concept 3.

The British Ecological Society survey listed approximately 50 wide-ranging items. The editor (Cherrett 1989) divided the 600 or so responding ecologists into two groups: practical holists and theoretical reductionists. I do not believe these dichotomies between holism and reductionism and that between theoretical and practical are very helpful. The most exciting of the concepts listed apply to all levels or to the interaction of levels, and any and all may have practical as well as theoretical aspects. I believe that my more comprehensive 20 concepts cover most of what is in the 50-item list.

I am sure that there are other concepts that might be added to my list, and I suspect that some of my choices may be considered by some ecologists as too hypothetical to have been included. I invite comments to further explore what concepts are most important to public knowledge of ecology (i.e., environmental literacy).

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